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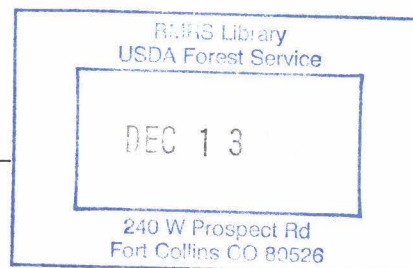
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PATHOGENS AS DISTURBANCE AGENTS IN CALIFORNIA FOREST ECOSYSTEMS

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INTRODUCTION

This paper summarizes the role, or function, of some major pathogens in California forest ecosystems. A general discussion of insect and pathogen contributions to, and effects on, ecosystems is presented, followed by more specific discussions of the functions of some individual pathogens, including dwarf mistletoes, annosus root disease, black stain root disease, and decay fungi associated with tree wounding.

AGENTS OF DISTURBANCE

Ecosystems are constantly changing. Some agents of change, or agents of disturbance, are natural, while others, such as fire suppression and management activities, are a result of human influences on the environment. The major natural disturbance agents affecting vegetative change in California forest ecosystems are fire, insects and pathogens, and windthrow/storm damage. This paper focuses on the role of some major pathogens (pathogens are agents, either living or non-living, that cause disease) as natural disturbance agents.

Most, but not all (introduced, exotic, insects and pathogens are the exception), insects and pathogens are normal components of the forest ecosystem. Their presence results in growth loss, reduced tree vigor, and tree death. Consequences of these effects depends on management objectives. The consequences are different in forests where the major objective is harvesting timber than in forests managed for other values, uses, and outputs. The death of a tree, as a result of insect or pathogen attack, represents the loss of so many cubic feet of timber. At the same time, the death of a tree may improve soil fertility, promote other vegetation, contribute to biological diversity, and create new habitat (Goheen and Hansen 1993, Haak and Byler 1993, Monnig and Byler 1992).

The insects and pathogens that kill trees serve as food for other living organisms. For example, birds feed on bark and wood-infesting insects. Various birds and mammals eat

the seeds of the true and dwarf mistletoes. Humans, as well as other mammals, consume many species of mushrooms, including those produced by fungi that cause tree diseases.

By killing trees, insects and pathogens create wildlife habitat. Birds use trees killed by insects and pathogens for nesting and foraging. Cavity-nesting birds depend on habitats in snags and heart-rotted trees. Insects and pathogens affect structural diversity by killing the more common tree species, and allowing replacement by other, resistant, tree species. They contribute to biological diversity. Selective killing of certain, susceptible, tree species opens the canopy; these openings provide space, light, and nutrients for a variety of other plant species (Franklin et al. 1989, Schowalter and Filip 1993).

Insects and pathogens can also have a negative effect on forest ecosystems. On occasion, especially when forests are stressed, or "unhealthy", outbreaks or epidemics of forest insects and pathogens can occur. These outbreaks can have a negative effect on ecosystem values. In addition to tree growth loss and mortality, these outbreaks can result in unwanted, or unexpected, changes in composition and structure of vegetation. The degree of disturbance caused during these outbreaks depends on the condition, or health, of the ecosystem affected. When ecosystems are stressed, or out of balance, insects and pathogens can cause growth loss, tree mortality, and changes in vegetation over millions of acres of forests each year.

Table 1. Average annual acres (commercial forests) affected by major insects and pathogens.

Insect/ Pathogen	Millions of Acres	Region Affected
Dwarf Mistletoes	22.6	Western
Root Diseases	16.8	Western
Bark Beetles	4.3	Western

Table 1 presents average annual acres of commercial forest affected by several major insects and pathogens in the Western United States (USDA Forest Service 1989). The resulting volume loss and mortality from insects and pathogens, over about 44 million acres, exceeds the loss due to forest fires by a factor of 10 during average years, and much more in drought years. These high levels of disturbance indicate stressed, or out of balance, ecosystems.

Human disturbance agents such as fire suppression and management activities can stress forest ecosystems, resulting in increased levels of insects and pathogens. Fire suppression has resulted in increased levels of dwarf mistletoe; trees with dwarf mistletoe brooms near the ground are more likely to be killed by fire, and other effects of the parasite (spike tops, stunted growth, resin-infiltrated stem cankers) increase flammability of infested stands (Alexander and Hawksworth 1975). Fire suppression has also resulted in dense, overstocked stands of lodgepole pine, resulting in increased levels of mountain pine beetle. Management activities have increased levels of root pathogens, especially annosus root disease and black stain root disease.

When insects or pathogens increase to levels that interfere with management objectives, they become pests. Insect or pathogen pests are symptomatic of an ecosystem out of balance (Monnig and Byler 1992). To determine whether the effects of an insect or pathogen are mostly beneficial, or mostly detrimental, you need to know the management objectives for the area. Insects or pathogens that reduce timber production in commercial forests are pests. The same insects or pathogens may be of no consequence in areas managed for non-timber values.

Some tree mortality, which is a natural process in forest ecosystems, can improve diversity in structure and composition. Tree mortality over large areas can be detrimental by reducing habitat for sensitive species, or by increasing fuel loads and increasing risk of loss from fire. The effects of insects and pathogens as disturbance agents on the forest ecosystem, both beneficial and detrimental, need to be considered, and incorporated into resource management practices.

PATHOGENS AS DISTURBANCE AGENTS

Dwarf Mistletoes

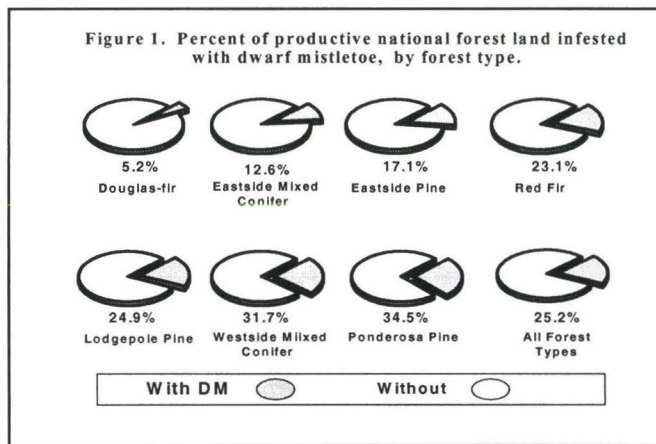
Dwarf mistletoes are parasitic plants, each species of which is specific to only certain host-conifer species (Hawksworth and Wiens 1970). They are obligate parasites, surviving only on living hosts. Being dependent on their host trees for water and nutrients, their effect is to slowly weaken and eventually kill their host. The effects of dwarf mistletoes are commonly accelerated by interactions with drought stress, overstocking, and insects.

The effects of dwarf mistletoes on non-commodity forest values vary. The effects on wildlife, for example, may be positive or negative, depending upon the particular ecological needs of the wildlife species. Dead trees provide nesting sites for snag-dependent bird species. Witches' brooms may provide cover and nesting sites for many birds and mammals. Large areas infested with mistletoes may have a more irregular, open forest canopy, favoring certain bird and mammal species over others. As the openings regenerate to either the same tree species or other tree species and brush, greater vegetation diversity will occur. This may result in profound changes in both stand structure and species composition (Johnson 1988). Squirrels, porcupines, birds, and other animals may, rarely, utilize dwarf mistletoe shoots as food (Hawksworth and Wiens 1972).

In timber stands, losses from dwarf mistletoe are due to reduced height and diameter growth of moderately to heavily infected trees, reduction in value due to poorer wood quality, and increased mortality of heavily infected trees. Estimates for height growth reductions for ponderosa pine are as high as 50% of normal growth for heavily infected trees (Hawksworth et al. 1991). Significant reduction in yields of stands occurs if they are infested early in their development and if no suppression measures are taken to reduce

the spread and intensity of the disease. Tree mortality is most often caused by the combined effects of mistletoe and cambium-feeding insects. Additional stress factors such as overstocking and drought increase the likelihood of mortality. During drought periods, dwarf mistletoe-infected trees are usually the first to die. During the 1976-79 drought, 50 to 75% of the pines that died were infected with dwarf mistletoe (Byler 1978, unpublished data Forest Pest Management).

Dwarf mistletoe is the most serious disease affecting ponderosa and Jeffrey pine, infesting 26% of the ponderosa pine type in California, Washington and Oregon (Bolsinger 1978). In California, this disease ranks second in importance to annosus root disease as the most damaging disease of white fir, affecting 30% of all white fir (California Forest Pest Control Action Council 1960). Dwarf mistletoe is a damaging disease in the eastside pine type forests, with about 9% of the ponderosa and Jeffrey pines surveyed from 1958-1966 infected (Smith 1983).



Recent summaries of national forest inventories (Forest Pest Management unpublished) indicate that over 2.2 million acres (25%) of productive national forest land in California are infested with dwarf mistletoe. Percent infection (percentage of acres with one or more trees per acre infected) varies by forest type, ranging from 5.2% in the Douglas-fir type, to 34.5% in the ponderosa pine type (Fig. 1).

Dwarf mistletoes can adversely affect recreation values by killing trees in campgrounds and other developed recreation sites. In addition to depletion of vegetative cover, the decay and canker fungi associated with dwarf mistletoe infections kill or weaken branches so that they are more susceptible to wind breakage, thus increasing the hazard to recreationists (Smith 1978).

Stand history is probably the most important factor governing the distribution and effects of dwarf mistletoes in ecosystems. Partial cutting generally intensifies the parasite in residual trees (Hawksworth 1961b). Many of the severely infested stands now present are the result of past selective logging practices in which infected overstory trees were either overlooked, or purposely left as undesirable commercially, resulting in infection of the subsequent understory. Sanitation and salvage harvests in mature stands for the express purpose of reducing dwarf mistletoe infections rates have had only limited success in reducing impact of the disease. In fact, repeated sanitation and salvage cutting often create the multiple-aged conditions which favor the spread of dwarf mistletoe (Barrett 1979).

Selection harvest creates multiple-aged or uneven-aged conditions which promote the spread of dwarf mistletoe (Barrett 1979, Seidal and Cochran 1981). Because dwarf mistletoes are long-lived obligate parasites which spread horizontally at a rather slow rate (average 1 to 2 feet per year) in even-aged systems, they are best adapted to survive and flourish in an uneven-age stand with a high proportion of susceptible hosts in both the overstory and understory. Spread and resulting damage is highest in stands of a single species, especially those with multi-layered canopies.

Levels of dwarf mistletoe will increase in multi-storied stands. In stands comprised of susceptible trees of different sizes, the crowns of smaller trees are continually exposed to inoculum from larger trees, resulting in infection of the upper crowns and reductions in growth (Parmeter 1978). This type of stand structure also results in a more rapid rate of spread of the dwarf mistletoe than through single-storied stands (Parmeter 1978). Thus, in mistletoe-infested stands, any silvicultural system which intermixes generations or sizes of susceptible host trees, will favor dwarf mistletoe infestation and spread.

The incidence of and damage from dwarf mistletoes will increase with small group selection harvesting. If the dwarf mistletoe interferes with management objectives, it becomes a pest and needs to be considered as a factor influencing management. Group selection on small areas will make it difficult to effectively control dwarf mistletoe. Any opening that increases sunlight in the stand will greatly increase the number of dwarf mistletoe plants, thus effectively increasing the inoculum available for infection of susceptible species (Hawksworth 1961a). Studies in California (Wagener 1961) suggest that partial sunlight is more favorable to the establishment of dwarf mistletoe on the host than relatively full or continuous sunshine. The number of visible plants can double within 4 years after thinning (Roth and Barrett 1985).

With single tree or small group selection, lightly infected trees are likely to be overlooked and left, perpetuating the mistletoe in the stand. An infected overstory tree left after a regeneration cut can provide enough dwarf mistletoe seed to infest about 1 acre of susceptible species in the understory (Parmeter and Scharpf 1972). With group selection, if the openings created are small and reforested with susceptible species, the trees in the openings will quickly become infected and will suffer heavy growth loss and mortality. The openings should be large enough to remove all infected trees. Otherwise, they should be reforested with resistant or immune species.

Unless infected overstory trees are intentionally retained, shelterwood and seed tree systems do not pose a significant risk of infecting the understory if the overstory is removed before the understory is large enough to become infected. However, under uneven-age systems, such as individual tree and group selection, where the future stand is continuously exposed to the currently infected overstory, infection of the new stand is assured and future growth loss and mortality will result. At the worst, the new stand may be prevented from ever reaching merchantable size and years later will have to be destroyed if the site is to produce wood fiber crops efficiently.

When management objectives are affected by heavy dwarf mistletoe infestation, regeneration harvests which remove the source of infection provide the only effective means for eliminating the disease and establishing healthy stands.

Annosus Root Disease

Annosus root disease, caused by the fungal pathogen *Heterobasidion annosum*, is the most important conifer root disease in California. Two strains of the fungus affect conifers, one specific to pines, juniper and incense-cedar, and the other specific to true firs, giant sequoia, hemlock, and spruce. Most annosus infection is caused by colonization of freshly-cut stump surfaces by wind-disseminated spores of the fungus. In true fir, colonization of basal wounds is also a source of infection. Because stump surfaces are the primary infection court, the occurrence and intensification of both strains of *H. annosum* is greatly increased by selective cutting and uneven-age management. This is especially true where regeneration of susceptible species on infested sites is favored, particularly true fir.

The strain of *H. annosum* which infects pine stumps moves via root contacts into the root systems of adjacent live trees and kills them by girdling the tree at the root crown. Direct mortality is often the result of bark beetle attack. This strain of the fungus may remain active for 30-50 years, passing the infection on to any conifer regeneration whose root system grows into contact with that of the infected stump, thereby rendering an infection center unproductive for an extended period of time (Smith 1984).

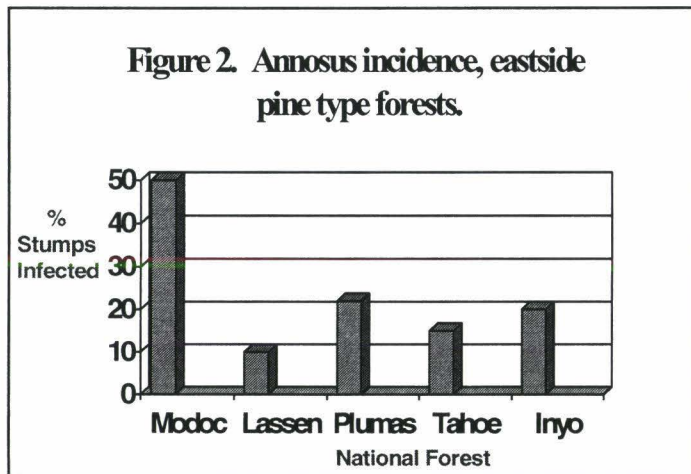
The strain of *H. annosum* which infects true fir causes a decay of the smaller roots and the heartwood of larger roots and the butt, but does not, as in pine, quickly kill the tree. In true fir, the result is a gradual decline (often lasting 10-20 years), resulting from decay of part of the root system and leading to windthrow, or death due to attack by fir engraver beetles. In true fir, wounds may also be colonized by the fungus, leading to substantial decay of the individual wounded tree, but not development of an infection center (Gast *et al.* 1991).

Annosus root disease, like other root diseases, may be beneficial. Death of small groups of trees results in patches of early succession vegetation within larger portions of forests, resulting in increased structural and compositional diversity. Standing dead trees may be utilized as habitat by cavity-nesting birds. The long term effect of annosus root disease is to create openings that slowly enlarge, producing a continuous supply of snags and down woody material. The openings may persist for many decades as the pathogen continues to kill any susceptible natural regeneration.

In California, the pathogen causing annosus root disease affects two million acres of commercial forest land and results in annual volume losses of about 19.3 million cubic feet (California Forest Pest Control Action Council 1988). A 1979-1980 survey

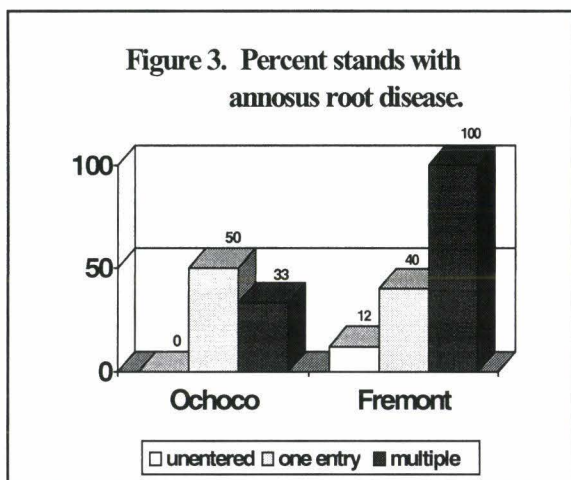
(Slaughter and Parmeter 1989) estimated that 4% (1.46 billion board feet) of the live true fir in 12 central and northern California national forests were infected by the pathogen. In addition to direct loss, annosus-infected trees provide a desirable habitat for bark beetles, flatheaded borers, and engraver beetles, resulting in more frequent, and more damaging, insect outbreaks (Smith 1984).

The root pathogen is widespread in eastside pine. Byler et al. (1978) found 60% of the pine stumps infected on the Fletcher Sale on the Modoc National Forest, and 1985 surveys of ten 8 to 15 year old sale areas on the same Forest showed 50% (range from 20 to 80%) infection (Kliejunas 1989a). These high levels are the result of past selective logging that occurred without borate treatment of stump surfaces to prevent infection.

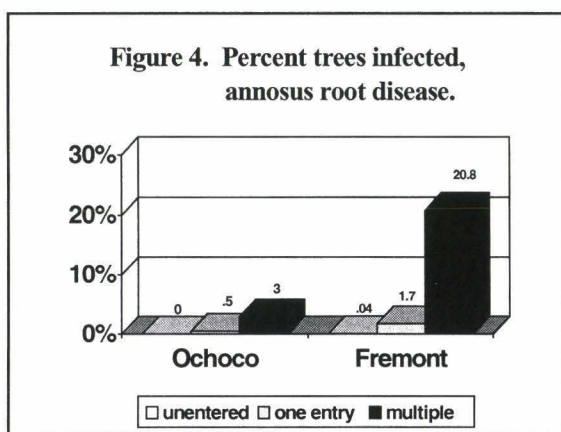


Recent surveys have found high levels of annosus root disease in the eastside pine type (Fig. 2). Levels, which are based on the percentage of pine stumps examined with conks of *H. annosum*, varied from 50% on the Modoc, 10% on the Lassen, 22% on the Plumas, 14% on the Tahoe, and 20% on the Inyo National Forest (Kliejunas 1989a, Kliejunas 1989b, Pronos and Harris 1991).

In unmanaged stands, annosus root disease usually occurs at low levels. However, stands that have had multiple partial cut entries tend to have a higher occurrence, especially in mixed conifer stands where true fir has been cut or wounded (Gast *et al.* 1991). The incidence and impact of annosus root disease increases substantially with multiple entries, characteristic of uneven-age management systems.



For example, in a study of true firs on the Ochoco and Fremont National Forests in Oregon (Goheen and Goheen 1989), 0 and 12% of the stands with no harvest entries had annosus root disease, 50 and 40% with one entry had disease, and 33 and 100% of the stands with multiple entries had annosus root disease (Fig. 3). Factors associated with an increase of *H. annosum* following stand entry include amount of disease present before entry, numbers of susceptible stumps created, and amount of tree wounding.



In addition to incidence of annosus root disease, severity of *H. annosum* was also greater in the entered stands than in the stands with no harvest history. The same study (Goheen and Goheen 1989) found that the percentage of true fir killed by *H. annosum* in the Ochoco and Fremont stands was 0 and 0.04% in stands with no entry, 0.5 and 1.7% in stands entered once, and 2.9 and 20.8% in stands with multiple entries (fig. 4).

Multiple harvest entries in stands with annosus root disease present, even at infection levels as low as 5%, can result in appreciable long-term yield losses. In a mixed conifer stand modeled on the Deschutes NF, total volume yield under uneven-age management was 73% of that obtained using a clear-cut harvest system (Petersen 1989). Any silvicultural system which retains infected overstory trees including selection cutting, sanitation and salvage cutting or shelterwood harvest (unless resistant species are used for reforestation) can result in continued or increased levels of stand infection. Clearcutting of infested stands and regeneration with resistant species can reduce the future incidence of annosus and other root rots.

Annosus root disease in high use recreation areas can cause serious problems in several ways. Diseased trees are often hazardous, causing death or injury to visitors, damage to permanent installations and property, and frequently resulting in expensive litigation. In addition to hazard, *H. annosum* may threaten trees essential to the setting, scenic value, and historic value of recreation sites. Some specific information on losses is available from Yosemite Valley. Fire control and grazing led to the establishment of dense stands of pine and incense-cedar in the Valley. The dense stands led to bark beetle infestation and subsequent removal of trees for bark beetle control. Trees were also removed to

make room for visitor facilities. The numerous stumps created were susceptible to invasion by *H. annosum* (Parmeter *et al.* 1978, Parmeter *et al.* 1979). More than 100 annosus root disease centers have been identified within developed sites in the Valley. Millions of dollars have been lost on subsequent property damage from falling trees and from removal of hazardous trees (West 1989).

Black Stain Root Disease

Black stain root disease is caused by the fungus *Leptographium wageneri*. This fungus has three strains or varieties, one affecting pines, one affecting single-leaf pinyon, and the third affecting Douglas-fir. Long distance spread, and initiation of new infection centers, is by insect transmission; root-feeding beetles and weevils are attracted to stressed, low vigor trees, carrying with them the spores of the fungus. The fungus infects the vascular system of the tree causing fairly rapid decline and death, often in conjunction with bark and engraver beetle attack. Black stain infected pines are predisposed to bark beetle attack. Populations of bark beetles in disease centers can reach levels at which healthy trees as well as diseased trees can be mass-attacked (Cobb 1988). Mortality of black stain infected Douglas-fir may be accelerated by engraver beetle and flatheaded borer attacks. Tree-to-tree root grafts or contact result in transmission of the black stain pathogen between trees within a disease center. Like annosus root disease, black stain infection results in centers of tree mortality, containing trees in various stages of decline.

The pockets of mortality, or "gaps", created can be beneficial. In mixed conifer forests of the central Sierra Nevada, selective killing of small stands of pure ponderosa pine, established after heavy logging in the early 1900's, enhances plant succession by allowing establishment of immune, shade tolerant, species such as white fir and incense-cedar (Byler *et al.* 1979). Black stain of Douglas -fir in conifer stands of northwestern California can result in an increase of hardwood trees, shrub species, and herbaceous plants, resulting in a habitat preferred by some wildlife species (Goheen and Hansen 1993). In eastside pine type stands, where alternative tree species are not available or suitable, the black stain centers remain as openings in the stand. The development of non-host understory shrubs and herbaceous plants in these openings can provide beneficial early successional wildlife habitat.

Most reports of black stain root disease conclude that its occurrence is related to site disturbance, overstocking, and wet sites (Cobb 1988). Infection centers are often associated with management activities such as selective harvest, thinning, or road construction which result in tree wounding or increased stress. Site disturbance attracts insect vectors of the disease (Hansen 1978). Dense, overstocked stands of ponderosa pine on the Modoc National Forest, established following logging and fires and subsequent fire control, appear especially suitable for black stain incidence. Incidence in ponderosa pine stands is correlated with wet or poorly drained soils, high amounts of organic matter, high C/N ratios, and increased exchangeable manganese (Wilks *et al.* 1983). Wetter sites exhibited higher spread rates (Wilks *et al.* 1985).

Losses of timber value due to black stain are not well documented. On the Georgetown Divide area of the central Sierra, the black stain/bark beetle complex has resulted in a loss of 57,000 cubic feet of wood per year (Byler *et al.* 1979). The disease is being found with increased frequency in eastside pine stands, usually associated with thinning or soil disturbance (Kliejunas 1992). Mortality of singleleaf pinyon pine caused by black stain root disease occurs over 20,000 to 30,000 acres of Bureau of Land Management lands in the southern Sierra (Smith 1983b), resulting in extreme fire hazard due to increased fuel loads.

Decay Associated With Wounds

Decay fungi are a natural part of the forest ecosystem, in both managed and unmanaged stands. These fungi are essential in the process of nutrient cycling. Wood decays of standing trees are beneficial for wildlife by providing sites for cavity nesting birds.

Wood decay fungi are not able to penetrate intact, living bark, but rely on any wound that provides an avenue into the inner tree. Natural wounds include fire scars, broken tops, lightning scars and branch stubs. The most common human-caused wounds are mechanical logging injuries and fire scars.

Wood decays of standing trees are detrimental if you are trying to grow trees for fiber or wood products. Decay associated with tree wounds is especially serious where repeated entries for thinning, single tree selection, slash disposal, prescribed burning, or other reasons occur in stands of susceptible species, particularly true firs. These wounds may either activate dormant fungal infections or provide entry for fungal spores. The location of the wound determines which decay fungi gain entry and how rapidly decay occurs.

Table 2. Infection and decay data for wounded white and red fir on the Klamath and Tahoe National Forests.

Forest	Wound Data			Tree Data	
	Total Trees	Total Wounds	Wounds Infected	Decay (bd. ft. volume) Percent	Range
Klamath	258	269	90%	5.7	0.1 - 31%
Tahoe	268	271	93%	7.6	0.1 - 47%

In 1981, true fir trees on the Klamath and Tahoe National Forests were felled, dissected, and analyzed for infection and decay (Aho *et al.* 1989). On the Klamath, 258 trees with 269 thinning wounds were sampled. Volume loss associated with decay was 5.7% of the gross merchantable Scribner board foot volume. The 268 sampled trees on the Tahoe had 271 thinning wounds, with a board foot volume loss of 7.6% (Table 2). A similar study on the Lassen

National Forest found a 12.8% board foot volume loss (Aho *et al.* 1983a).

These results suggest that true fir stands in California will experience substantial volume losses from decay if wounding of residual trees is not minimized during stand entry. Although procedures are established to reduce logging injury (Aho *et al.* 1983a, Aho *et al.* 1983b), each stand entry will allow the potential introduction of more decay, especially repeated single tree selection methods. Long-term results may include tree mortality, tree failure, or the loss of wood volume.

Therefore, uneven-age management systems, especially single tree selection which involves frequent entries and limited room for equipment maneuverability, would be expected to result in a significant amount of decay due to tree wounding. Similar, and perhaps worse, results for partial cutting with cable-logging systems might be expected, because in addition to the potential for basal wounds, wounding higher up on the bole and top-breakage would likely occur with selective cable logging.

SUMMARY

Insects and pathogens can have beneficial or detrimental effects on forest ecosystems. As natural components of ecosystems, they provide food, create wildlife habitat, affect structural diversity, and contribute to biological diversity. In stressed forest ecosystems, insects and pathogens can cause unwanted or unexpected changes. When insects or pathogens increase to levels that interfere with management objectives, they become pests. Levels of some pathogens, such as dwarf mistletoes, will increase with uneven-aged management. Increased stand entries and resulting site disturbance will favor increased levels of annosus root disease, black stain root disease and decay fungi associated with tree wounding. The resulting effects need to be considered in long term management decisions.

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